THE INCUBATION MOUND AND HATCHING SUCCESS OF THE NICOBAR MEGAPODE *MEGAPODIUS NICOBARIENSIS* BLYTH

(*With four text-figures and one plate*)

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Key words: Incubation mounds, Nicobar megapode, hatching success, megapodes, *Megapodius nicobariensis*

Incubation mounds of the Nicobar megapode *Megapodius nicobariensis* were constructed with sand or sand with plant materials, such as leaves, twigs and bits of decomposing wood. Usually, the site selected for a new incubation mound was a fallen log, tree stump, or the decomposing roots of a tree. Mound construction begins with the birds either digging a pit at the site or by covering the decomposing log or tree stump with soil and litter. The mean egg-laying interval was 14.91 ±1.43 days, the average number of eggs laid in a mound was 4.5 ±0.6 eggs, but it significantly varied between the years and the average clutch size of the Nicobar megapode was 2.75 ±0.35 eggs. Moderate rainfall in the dry season enhances egg production. Microbial activity appears to be the primary source of heat within mounds. The size of the mound was positively correlated to the temperature within the mound. The average incubation temperature was 32.44 ±0.21 °C and the average incubation period was 74.73 ±0.52 days. There was, however, no significant relationship between the mound size and hatching success of the Nicobar megapode.

INTRODUCTION

Megapodes are unique among birds because they incubate their eggs in mounds of rotting leaves or in burrows in geothermally heated ground (Frith 1956, Dekker and Wattel 1987, Jones 1988, Dekker 1990). Perhaps the best-studied aspects of the Megapodiidae are the incubation conditions within mounds and communal nesting grounds (Frith 1956, 1959, Crome and Brown 1979, Seymour *et al.* 1986, Booth 1987, Seymour *et al.* 1987, Dekker 1988, Jones 1988).

Within the Megapodiidae, there exist two groups, burrow nesters and mound builders with variations in the incubation and breeding strategies. Burrow nesting species like *Macrocephalon* and *Eulipoa* lay eggs at communal nesting grounds where sun or volcanic activity provides heat for incubation (Dekker 1988, 1990, Heij *et al.* 1997). *Talegalla, Aephypodius, Alectura* and *Leipoa* build incubation mounds of forest litter where organic decomposition provides necessary heat (Dekker 1990). Of the 13 species that comprise the genus *Megapodius*, 10 are mound builders, two are burrow nesters, and one nests in both burrow and mound (Jones *et al.* 1995). The Nicobar megapode *Megapodius nicobariensis*, a monomorphic mound building megapode (Plate 1, Figs 1,2), endemic to the Nicobar Islands in the Bay of Bengal, builds incubation mounds of sand, loam, coral bits and rotting vegetation, within which eggs are laid. Incubation mounds of the Nicobar megapode vary in type, size and location (Dekker 1992, Sankaran 1995, Sankaran and Sivakumar 1999, Sivakumar and Sankaran, in press). Some mounds have a greater admixture of vegetative material, while others have a greater amount of sunlight falling on them, which suggests that the source of heat varies between mounds. In this paper, we address the questions consequently raised: which sources of heat provide the most stable incubation conditions? Do sources of heat that create suitable

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incubation conditions within mounds vary with mound type, location and dimensions? And do heat sources and mound dimensions have a bearing on the number of pairs that use a mound, the number of eggs laid, and hatching success?

STUDY AREA

The Andaman and Nicobar Islands (6° 45' to 13° 41' N, 92° 12' to 93° 57' E), in the Bay of Bengal, arch from Arakan Yoma, Myanmar in the north to Sumatra, Indonesia in the south (Saldanha 1989; Fig. 1). These islands cover an area of 8,249 sq. km with a coastline of 1,962 km. The Andaman group with more than 325 islands (21 inhabited) covers an area of 6,408 sq. km. The Nicobar group with over 24 islands (13 inhabited) covers an area of 1,841 sq. km (Singh 1981, Saldanha 1989).

We studied the ecology of the Nicobar megapode between December 1995 and July 1996, December 1996 and June 1997, September and October 1997, and February and May 1998. The study period includes three dry seasons (peak period of egg laying) and part of one wet season. Our study area was on the coast at the southern tip of Great Nicobar Island. The intensive study area was a narrow strip of forest, of width varying between 40 and 300 m and length about 4 km, which was bisected by a disused metalled road, ending at the light house at Indira Point. The beach forms the boundary to the study area in the east, and wetlands or forests that are inundated during the monsoons form the boundary to the west. The soil within this strip of coastal forest was sandy and loamy, and the dominant trees were *Barringtonia asiatica*,

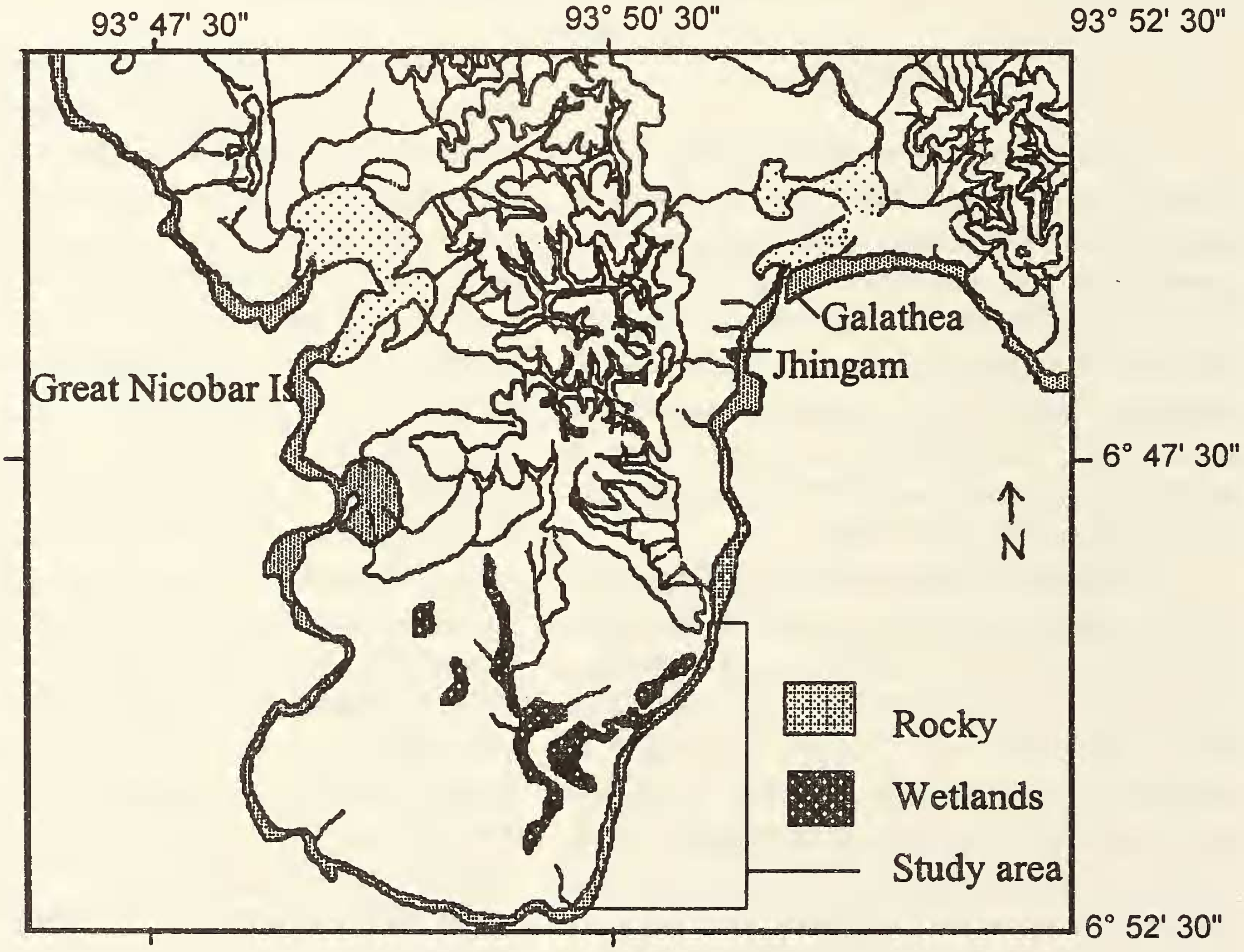

Fig. 1: Southern part of the Great Nicobar Island showing the study site

Sivakumar, K. and R. Sankaran: Nicobar megapode *Megapodius nicobariensis* PLATE 1

Fig. 1: Nicobar megapode on the mound it has built

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Fig. 2: Another incubation mound of the Nicobar megapode

B. racemosa, *Terminalia bialata*, *Terminalia catappa*, *Syzygium samarangense*, *Thespesia populnea* and *Macaranga* spp. The study area had dense stands of *Pandanus tectorius* and *P. odoratissimus* in patches, and the road was fringed by stands of *Lea angulata*, *L. grandifolia*, and *Dracaena* spp. There were a few patches of open ground with little vegetation. The forest forming the boundary of the study area to the west had wet clayey soil and was covered with *Areca* spp. as well as trees like *Ixora barbata*, *Pongamia pinnata*, *Alstonia kurzii*, *Adentania paranina*, *Aisandra butyracea*, *Horsfieldia irya*, *Myristica andamanica*, and *Celtis timorensis*.

METHODS

At the start of the study or whenever a new mound was constructed, detailed drawings of the mounds were made to scale using measuring tapes and a compass, and salient characteristics such as living trees and dead logs or tree stumps were plotted on these. The basal circumference, height and diameter of the mounds were measured once a month. Mounds were uneven in shape with a cone-like appearance. The mound size, expressed as volume, was derived from the equation for the volume of a cone: $1/3\pi r^2 h$ where 'r' is the radius and 'h' the height, giving the approximate volume of the mound.

All the incubation mounds in the study area were visited at least twice a day, in the morning and in the evening and occasionally during midday, to identify whether megapodes had worked on the mounds, and what type of activity they had engaged in. At four mounds, the megapodes were intensively observed, following the focal animal sampling method (Altmann 1974), from observation hides. Observations from the hide usually started before the arrival of birds at the mound (at 0500 to 0530 hrs) and ended after the birds left the mound. Observation recommenced at about 1400 hrs and was carried on till dusk. The activities of the birds were classified into: visit, pit digging, egg laying, raking, covering, pits-filled, and random activity.

In 1996, four temperature probes were implanted at depths between 20 and 75 cm, in seven mounds that had been selected for intensive studies. However, after about two months these probes malfunctioned, probably due to high humidity and rainfall. In 1997 and 1998, a temperature probe placed at the tip of a one metre long steel tube was inserted to depths of 30, 60 and 90 cm to measure the temperature. Using this method the temperatures were measured once a month for all the mounds in the study area, every 15 days for the target mounds, both in the morning and evening. Occasionally the temperature of the mound was also measured during midday.

Microbial activity was measured using a soil respirometer (PP Systems EGM-1 Environmental Gas Monitor with a SRC-1 Soil Respiration System), assuming that in those mounds where microbial activity was high, greater amounts of CO_2 would be emitted. The soil respirometer measures the CO_2 change in a fixed volume over a known time and fits a quadratic equation to the data to arrive at a value 'SR' which is the soil respiration rate in $gCO_2/m^3/hr$. Soil respiration was measured once every 10 or 15 days for the seven mounds that were under intensive study. Like temperature, data on the soil respiration of mounds was collected both in the morning and evening.

The intensity of light falling on the mound at different times of the day was measured using a luxmeter. The amount of Photosynthetic Active Radiation (PAR) falling upon the mound and PAR absorbed by the mound were measured using Sunfleck Ceptometer (Decagon, Pullman, WA). This was also measured outside the mound. The gap in the canopy cover above the mound was measured using a concave mirror that was uniformly graduated.

Soil samples were collected from the surface of the mound and then sun dried for an hour.

Percentage of humidity was measured by using the following formula:

Humidity (%) = [(Wet soil weight - Sun dried soil weight) / Wet soil weight] x 100

During the breeding seasons of 1996, 1997 and 1998, thirty-seven mounds were monitored. When an egg was laid, it was dug out and weighed to the nearest gram using a spring balance. Eggs were also measured with Vernier callipers and marked with a number and date using an HB graphite pencil. After weighing and marking, the eggs were reburied in the same egg chamber and the mound was rebuilt. For identification, a stick was placed adjacent to the egg chamber. During 1997 and 1998, thirty-four eggs were directly marked and monitored. The marked eggs were monitored by rechecking them once every 15 days. At the beginning of 1998, all the mounds were thoroughly checked with the help of mound maps of 1997, where the locations of eggs were clearly plotted. Successful hatching of eggs was evident from eggshell fragments and pieces of shell membrane where the eggs had been. Emergence of the chick from the egg during hatching and its subsequent activity was observed by placing a glass plate adjacent to the egg on the day of egg laying. In 1998, a total of seven eggs were monitored for the same. Eggs which remained in the mounds for the entire breeding season, or those which did not hatch for 100 days were opened and examined.

RESULTS

Description of incubation mound of the Nicobar megapode

Of the 38 incubation mounds present in the study area between 1996 and 1998 (Table 1), three were type 'A' incubation mounds built on an open spot away from trees, three were type 'B' incubation mounds built against a large living tree, and 25 were type 'C' incubation mounds built on or around a dead log or stump. Of the remainder, four incubation mounds were type 'BC' (built against the buttress of a partially living tree, or with a dead log in it), of which two later became type 'C' in 1998 because the trees died out completely. One incubation mound was type 'AB' as it was built in the open with two living *Pandanus* palms in it (Table 1). Two incubation mounds were unusual, as they were built against the edge of the disused metalled road that bisected the study area (type 'R'). Among the16 incubation mounds that were newly constructed during the study period, 13 were type 'C' incubation mounds, one was a type 'B' incubation mound, and two were built against the road (Table 1).

The construction and maintenance of an incubation mound involves several activities. Usually, the site selected for a new incubation mound is a fallen log, tree stump, or the decomposing roots of a tree. The megapodes began construction of the new incubation mound either by digging a pit if the site was over decomposed roots or by covering the decomposing log with soil and litter raked in from the surrounding areas. The process of raking soil and litter on to the site, or the piling up of soil and other material over the pits, soon resulted in the formation of a new incubation mound.

Temperature and soil respiration in and out of the incubation mound

Mean core temperature at the depth of 50-60 cm in an incubation mound was 31.94 °C (SE 0.075, n=634). It was higher than the forest ground where it was 28.72 °C (SE 1.66, n=105) at the same depth. The mean soil respiration rate (SR in $gCO_2/m^3/hr$) on the active incubation mound was 5.55 (SE 0.13, n=920), which was always higher than that on the abandoned incubation mound (SR= 2.88, SE 0.92, n=140) as well as the normal ground (SR = 3.7, SE 0.86, n=130).

Incubation period and optimal incubation temperature

Incubation temperature (mound core temperature) of the 34 egg chambers in 16 different

Table 1: The history of incubation mounds of the Nicobar megapode in the study area

S. No.	Mound Code No.	Birds/ year	First located on	End date	Status	Type	Distance from the shore (m)	Average size[1] (cu. m)
1	10	10	5-Jan-1996	May-1998	PS	A	25	40.24
2	4	7	3-Jan-1996	May-1998	PS	BC	25	15.31
3	13	7	5-Jan-1996	May-1998	PS	C	240	12.88
4	16	-	17-May-1997	May-1998	NF	A	5	12.12
5	12A	3	3-Feb-1996	May-1998	NF	C	185	9.14
6	14	11	28-Jan-1996	May-1998	PS	C	105	8.98
7	12	4	5-Jan-1996	May-1998	PS	C	205	8.17
8	8	18	3-Jan-1996	May-1998	PS	BC	27	8.02
9	10B	3	7-May-1997	May-1998	NC	C	132	6.98
10	5	2	3-Jan-1996	Jan-1996	PS	C	85	6.88
11	9	16	5-Jan-1996	May-1998	PS	BC	83	6.67
12	12B	2	28-Jan-1997	Apr-1998	NF	C	190	6.26
13	3	7	3-Jan-1996	May-1998	PS	BC	20	4.03
14	2	2	3-Jan-1996	Feb-1997	PS	A	15	3.98
15	15	2	5-Feb-1996	Mar-1998	NF	C	160	3.74
16	9A	4	30-Jan-1996	Feb-1998	PS	AB	95	3.11
17	8C	1	11-Apr-1998	May-1998	NC	C	42	2.96
18	6	6	3-Jan-1996	May-1998	PS	C	74	2.74
19	1	5	3-Jan-1996	May-1998	PS	C	52	2.29
20	9C	9	13-Feb-1997	Apr-1998	NC	C	80	2.02
21	7C	1	26-Sep-1997	Mar-1998	NC	B	22	1.75
22	8A	1	19-Mar-1996	Mar-1998	NF	C	110	1.57
23	8D	1	11-Apr-1998	May-1998	NC	C	6	0.99
24	7	5	3-Jan-1996	May-1998	PS	C	105	0.93
25	1B	2	23-Apr-1997	May-1998	NC	C	15	0.76
26	10D	1	27-Mar-1998	May-1998	NC	C	8	0.76
27	11	2	5-Jan-1996	May-1998	PS	C	195	0.76
28	7A	2	3-Jan-1996	May-1998	PS	C	105	0.66
29	13A	1	19-Mar-1997	Feb-1998	NC	R	120	0.64
30	10A	2	7-May-1997	May-1998	NC	C	35	0.50
31	9B	1	10-Feb-1996	Feb-1998	NC	B	10	0.49
32	8B	1	27-Mar-1998	May-1998	NC	C	10	0.39
33	13B	1	19-Mar-1997	Feb-1998	NC	R	120	0.38
34	11A	2	12-Feb-1996	Feb-1998	NC	C	180	0.37
35	1A	3	16-Apr-1997	May-1998	NC	C	15	0.35
36	6A	3	21-Mar-1996	Apr-1998	NF	B	30	0.32
37	7B	1	6-Feb-1998	May-1998	NC	C	20	0.26
38	10C	1	5-Sep-1997	Feb-1998	NC	C	130	-

NC= New construction; PS= Present at start of study, NF= Newly found.

[1] As mounds change in size over time, the mean value for all mound size data collected during the study is given.

mounds was monitored, and the incubation period for 30 eggs determined. The remaining four eggs did not hatch. The shortest incubation periods were 70 days (n=1 egg) and 72 days (n=6 eggs) and the longest incubation period was 81 days (n=1 egg). The mean temperature of the egg chamber for successful hatching was 32.44 ±0.21 °C (n=30). The mean incubation period of the monitored eggs was 74.73 ±0.52 days. Though the data (Fig. 2) indicates that as temperature decreased the incubation period increased, there was no significant negative correlation between the length of incubation period and incubation temperature ($r = -0.31$, $n=30$, $p=0.095$). Moreover, as eggs incubated at different temperatures hatched in almost the same period, it also indicates that minor fluctuation in the temperature of the egg-chamber did not affect the incubation period significantly.

Effects of incubation mound size on incubation temperature

The effect of mound size on the incubation temperature in 37 incubation mounds was studied. The sizes of the 37 incubation mounds varied from 0.15 cu. m to 40.24 cu. m, with a mean size of 4.78 cu. m (SE 1.19). As mound size increased, the temperature of the mound also increased (Fig. 3) at the depth of 30 cm ($r=0.162$, $n=518$, $p<0.001$), 60 cm ($r=0.177$, $n=532$, $p<0.001$) and 90 cm ($r=0.307$, $n=526$, $p<0.001$). Within a mound there was some fluctuation in the incubation temperature, irrespective of sizes (Fig. 3).

Table 2: Average temperature (in °C) of the mounds at various depths

	Ambient	Surface	Upper layer	Middle layer	Deep layer	Deepest layer
Mean	28.17	27.57	29.91	30.65	31.94	32.51
n	735	745	196	618	634	628
SE	0.065	0.055	0.177	0.074	0.075	0.072

Role of sunlight in incubation temperatures

Intensity of the light (lux value) significantly enhanced the ambient temperature ($r=0.24$, $n=168$, $p<0.01$) and surface temperatures of the mound ($r=0.25$, $n=168$, $p<0.01$) but not that of the mound core ($r=0.053$, $n=96$, $p=0.610$). However, there was a positive correlation between the surface and the mound core temperature ($r=0.23$, $n=626$, $p<0.001$). The mean ambient and surface temperatures were always lower than the mound temperatures at different depths (Table 2).

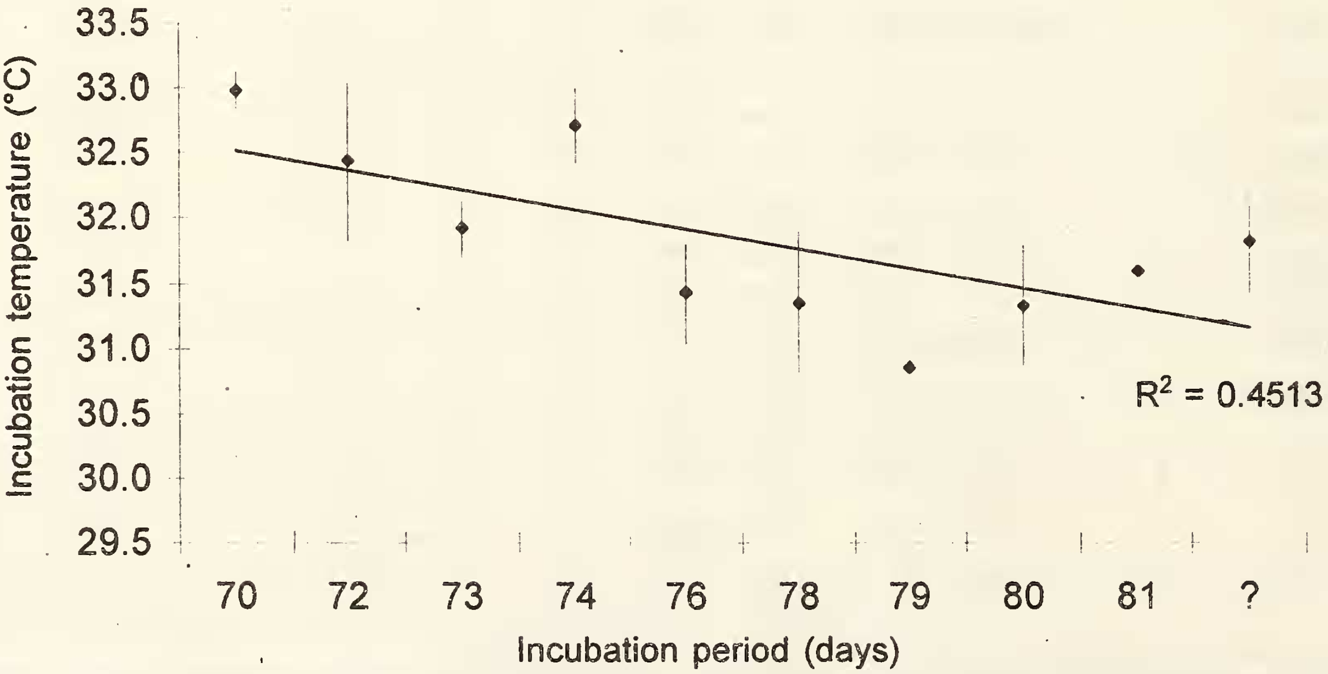

Fig. 2: The relation between the incubation temperature (°C) and incubation period (days) of egg of the Nicobar megapode (Standard error of the mean shown as error bar, '?' are unhatched eggs)

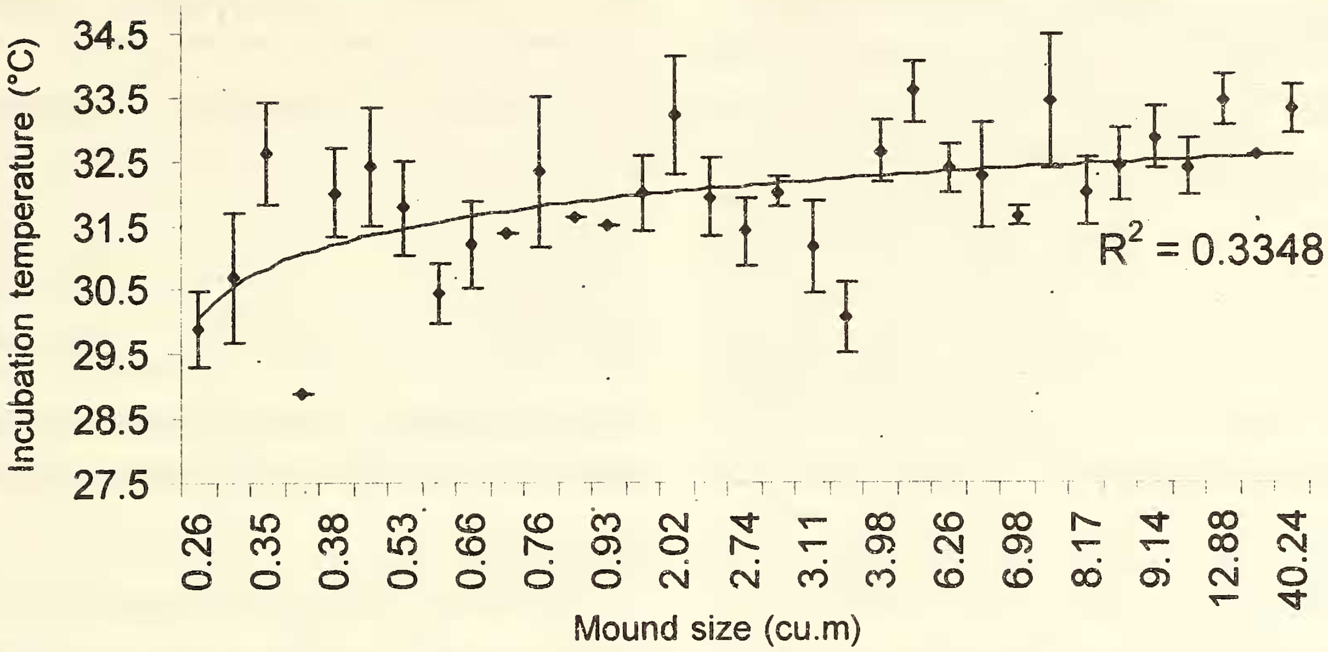

Fig. 3: Relation between mound size and incubation temperature of the Nicobar megapode (Standard error of the mean temperature shown as error bar)

Role of microbial activity in mound incubation temperatures

There was a significant positive correlation between soil respiration rate and the incubation temperature of the mound ($r=0.15$, $n=204$, $p=0.02$; Fig. 4).

Effect of moisture content of the mound on incubation temperature

Moisture content of the mound soil highly influenced the intensity of the mound temperature. An increase in the moisture content of the soil resulted in an increase in mound temperature at the different depths studied, as follows: 30 cm ($r=0.272$, $n=166$, $p<0.001$), 60 cm ($r=0.407$, $n=166$, $p<0.001$) and 90 cm depth ($r=0.534$, $n=166$, $p<0.001$). We did not estimate the soil respiration rate when the moisture content of the soil was estimated, as a result of which the influence of moisture on the microbial activity of the soil could not be established.

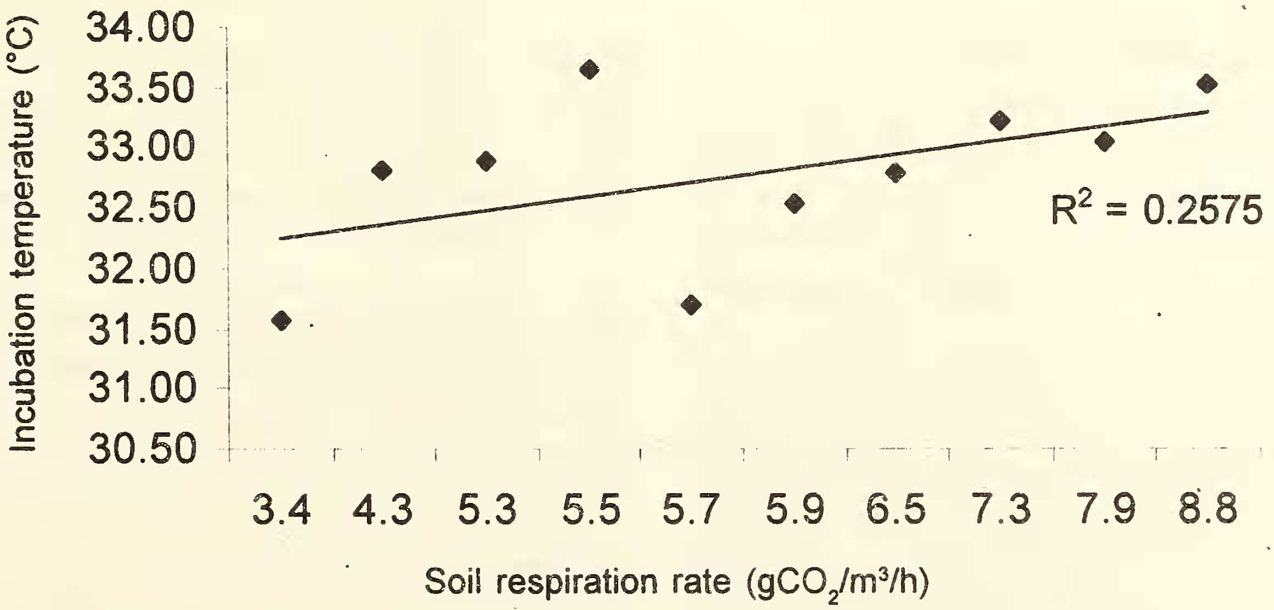

Fig. 4: Effects of microbial activities on the incubation temperature in the mounds of the Nicobar megapode

Egg-laying behaviour of the Nicobar megapode

The egg-laying interval between two consecutive eggs and the clutch size of the Nicobar megapode was estimated from 28 colour-marked birds. The mean egg-laying interval between two consecutive eggs of the Nicobar megapode was 14.91 ±1.43 days (n=11 intervals in 17 eggs). The average number of eggs laid in a mound was 4.5 ±0.6 (n=58) but it significantly varied between the years (Kruskal Wallis H test, c^2 =8.203, df=2, p=0.017). Clutch sizes of the Nicobar megapode varied between one to four eggs per season or year. We collected data on the clutch size of seven colour-marked pairs in 1997 and five in 1998. Of the twelve colour-marked pairs, five pairs laid four eggs per year in one or two mounds and remaining pairs laid two to three eggs in one or two mounds. In general, the average clutch size of the Nicobar megapode was 2.75 eggs (SE 0.35, n=12).

The peak period of the egg-laying was between February and May, during which 86.6% and 84.7% of the eggs were laid in 1996 and 1997 respectively. Egg-laying was not observed during the wet season of our study (September and October of 1997). The total number of eggs laid in all the mounds of the study area in the year 1996, 1997, and 1998, were 112, 124, and 35, respectively.

Incubation mound size and egg-laying

Of the 38 incubation mounds that were active in the study area in 1996, 1997, or 1998, eggs were laid in 35 mounds. Of these, only 10 incubation mounds were used in all the dry seasons between 1996 and 1998 for egg laying.

According to the sizes, mounds were grouped into the four categories, namely very small, small, medium and large mounds. The very small sized incubation mounds (<1 cu. m) had the least number of eggs laid in them (Table 3). Small sized incubation mounds (1-5 cu. m) had an average of 4.05 eggs laid in them, medium sized incubation mounds (5-10 cu. m) contained an average of 5.93 eggs, while large sized incubation mounds had the most number of eggs (Table 3).

Table 3: The mean number of eggs laid in different size classes of mounds throughout the study period

Size of incubation mound	No. of mounds	Eggs laid/ year (±SE)
< 1 cu. m	10	2.3 ±0.77
1.1 – 5 cu. m	7	4.05 ±0.60
5.1 – 10 cu. m	7	5.93 ±1.55
< 10 cu. m	3	6.83 ±1.69

Hatching success

Hatching success was determined in 32 incubation mounds in 1997, where one to five eggs were laid in 13 incubation mounds, six to ten eggs in 6 incubation mounds, and more than ten eggs in 4 incubation mounds. Five of the incubation mounds were not used for egg-laying in 1997, and the number of eggs laid in the remaining four incubation mounds could not be determined. Mean hatching success in the incubation mounds in 1997 was 57.26%. Of the 124 eggs laid in 23 mounds, 10.48% of eggs did not hatch and those eggs were unearthed in the next season; 29.84% eggs disappeared or were predated, and the fate of 2.42% of eggs was not clear (if these eggs successfully hatched then the hatching success was 59.68%).

Small incubation mounds had less number of eggs, while medium sized incubation mounds were used by the birds for more egg-laying (Table 4). However, there was no relationship between the incubation mound size and hatching success (Table 4).

Table 4: Hatching success of eggs in different sizes of incubation mound of the Nicobar megapode in 1997

Size of incubation mound	n	Eggs laid (±SE)	Hatching success % (±SE)
< 1 cu. m	9	1.9 ±0.5	74.1 ±14.5
1.1 – 5 cu. m	7	6.6 ±1.8	52.6 ±8.1
5.1 – 10 cu. m	4	9.5 ±3.1	68.1 ±11.0
> 10 cu. m	3	7.7 ±1.7	59.6 ±7.1

DISCUSSION

Incubation conditions within incubation mounds

Incubation mounds of the megapodes are amongst the largest structures made by any non-colonial animal, and represent the harnessing of the energy produced by microbial respiration (Seymour *et al.* 1986, Jones 1989), and/or solar radiation (Frith 1956, 1959) by concentrating suitable material to provide optimal incubation conditions at about 33-34 °C (Dekker 1992). In some species, microbial respiration and solar radiation may be used sequentially to create incubation conditions (Frith 1956, 1959). Seymour (1985) proposed that heat production and heat loss tends to stabilise mound temperatures at an equilibrium state due to the great thermal inertia of mounds once they cross a certain size and as they maintain adequate moisture content with the regular incorporation of fresh organic material into the mound. This model has gained further support from other studies (Jones 1988, Jones and Birks 1992).

Mound temperatures usually stabilise between 32-35 °C (Jones *et al.* 1995), which is consistent with that of the Nicobar megapode (32.44 °C). Incubation temperatures in mounds show considerable fluctuation, and while the negative effects of these fluctuations on eggs are largely offset by a variable incubation period (Booth 1987), there are strategies to balance both heat loss and gain (Jones 1989, Jones and Birks 1992).

However, the data from the incubation mound of the Nicobar megapode does not fully fit with the assumptions mentioned above by Seymour (1985). Firstly, the size of the incubation mound can vary in height from 10 cm up to 2.1 m and in basal circumference from 7 to 45 m (Sankaran 1995). Secondly, the proportion of organic material in an incubation mound varies due to location of the mound, and the availability of materials around it. And thirdly, the gap in the canopy above the incubation mound varies, resulting in differences in the amount and duration of sunlight falling on it. This might indicate that the heat sources which create suitable incubation conditions within the mound may vary, with some incubation mounds appearing to rely more on sunlight and others on organic decomposition (Sankaran and Sivakumar 1999).

Solar energy, however, probably only optimises the incubation mound temperatures. Though the canopy above an incubation mound was less than the canopy above non-mound areas, direct sunlight fell on the mounds for very short periods, with the result that both ambient temperature and incubation mound surface temperatures were always lower than incubation mound core temperatures. Thus, the role of solar energy appears to be restricted to warming the surface of the incubation mound, whereby dissipation of heat was reduced.

Microbial respiration is the primary source of heat harnessed by most mound building megapodes (Jones *et al.* 1995). A clear relation exists between the incubation temperatures and the organic activity as evidenced from soil respiration in the Nicobar megapode as well. Microbial respiration has a linear relation to the temperature of the incubation mound at deeper layers. However, incubation mounds with higher levels of soil respiration did not necessarily have higher temperatures. Two factors could be responsible for this. Firstly, there might be differences in the amount of heat produced by decomposition due to the kind of vegetative materials added to the incubation mound. Secondly, the rate of heat loss probably differs between incubation mounds, caused by differences in the proportion of surface area to the volume of the incubation mound, or to the amount of moisture content within the incubation mound (Jones *et al.* 1995), or the amount of sunlight or radiation from the beach falling on the mound.

Mound size, egg-laying and hatching success

The optimisation of incubation conditions in large incubation mounds is reflected in an overall trend of a greater number of pairs using such mounds, and consequently, a greater number of eggs being laid in them. However, some small mounds had a greater number of eggs, and some larger mounds had fewer eggs, indicating that size is not the only criterion. The quality of the incubation mound, and the number of pairs using an incubation mound, which appears to be somewhat independent of incubation mound size, are probably other determining factors.

As optimal temperature was consistently present in large mounds, one would expect that eggs in large incubation mounds are more likely to hatch successfully than in smaller incubation mounds. However, hatching success of the Nicobar megapode does not reflect this trend. This study reveals that there was no significant relationship between the incubation mound size and hatching success. Very small and medium sized incubation mounds showed more hatching success than the small (1-5 cu. m) sized ones. The probable reason for the lower hatching success in the small sized incubation mounds (1-5 cu. m; Table 4) was the large number of birds that used them. Greater digging activity and consequently greater exposure of eggs to the atmosphere was a possible factor for lower hatching success. Secondly, more mound activities may attract more predators, especially monitor lizards. About 30% of megapode eggs were predated in 1997, when activities at the mound were also the most. Clutch size of the Nicobar megapode was lower than other mound building megapodes (Jones *et al.* 1995).

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